

Larval crowding during an insect outbreak reduces herbivory pressure on preferred shrubs in a warmer environment

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ARTICLE INFO

Keywords:

Climate change
Gompertz
Herbivore pressure
Host plant preference
Insect outbreaks
Sub-arctic

ABSTRACT

With warming climate many species are predicted to shift their distributions toward the poles. However, climate change models developed to predict species distributions do not always incorporate interactions between them. The northerly shift of the boreal forest and associated dwarf shrub communities will be directly affected by warming. But warming will also indirectly affect plant communities via impacts on the intensity and frequency of associated insect outbreaks. We present a general model exploring plant host herbivory in response to the balance between insect crowding, host consumption and climate. We examined how these factors dictate the feeding preference of *Epirrita autumnata* larvae during an outbreak on dwarf shrub vegetation in Sub-arctic Fennoscandia. Data were collected from an outdoor experiment investigating future climate change scenarios (elevated CO₂ and temperature) on the dwarf shrub community that included deciduous (*Vaccinium myrtillus*) and evergreen species (*V. vitis-idaea* and *Empetrum nigrum*). We observed that larval crowding was independent of treatment under outbreak conditions. We also tested and confirmed model predictions that larvae would prefer monospecific stands of either deciduous shrubs or its evergreen competitors. For current climate conditions, larvae had a preference to consume more deciduous shrubs in mixed stands. However, at elevated temperature bilberry consumption and herbivore pressure was lower, particularly in mixed stands. Our results show that during future warming, *E. autumnata* herbivory could promote the success of thermophile deciduous species and possible northward migration. Insect behaviour and preferences should therefore be considered when predicting future vegetation movements responding to warming.

1. Introduction

Spatial bioclimatic models predict and some studies already demonstrate range expansion towards the poles and higher elevations of thermophile vegetation under climate change scenarios (Lewis, 2006; Post et al., 2009; Callaghan et al., 2013). However, this depends on whether the ability of species to disperse matches the displacement of corresponding climate envelopes. At the same time these models are constrained by the absence of attention to ecological interactions (Araújo and Luoto, 2007; Berg et al., 2010; Van der Putten et al., 2010). In northern latitude forests, the success of a plant species may be strongly coupled to herbivory, particularly during outbreaks of forest defoliating insects and bark beetles (Karlsen et al., 2013). These,

together with the direct effects of climate on plants will be highly relevant to consider when predicting effects of a changing climate on boreal forest ecosystems (Niemelä et al., 2001; Hicke et al., 2012). Responses to herbivory and climate may include changes in plant community structure and biomass (Olofsson et al., 2009) and range (Van Bogaert et al., 2009).

Host plant preference by herbivores is particularly important at vegetation boundaries (Janz and Nylin, 1997). Climate change factors (including temperature and CO₂) and herbivory itself directly influence plant chemistry and defences, dictating subsequent host preference of the herbivore (Wilf et al., 2001; Haukioja, 2005). A host plant species targeted by a particular herbivore can be competitively disadvantaged and must balance resources between herbivore and plant competition

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<https://doi.org/10.1016/j.agrformet.2018.08.016>

Received 4 February 2018; Received in revised form 20 August 2018; Accepted 21 August 2018

Available online 29 August 2018

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(Agrawal et al., 2006). However, this balance will be influenced by the intensity of herbivory, which will also be modulated by climate (Andrew and Hughes, 2007; Post et al., 2009).

It is generally predicted that the rate of herbivory may intensify with future warming (Tylianakis et al., 2008). However, Barrio et al. (2016) investigated how future warming could influence herbivores and herbivory of tundra plants by the Arctic moth (*Gynaephora groenlandica*) in the Yukon, Canada. They showed that the performance of insects themselves was compromised by warming and that the insects also shifted to consuming faster growing plants high in nitrogen. Further, the insect's typically preferred host plant species (*Salix arctica*) also responded negatively to warming. Hence predicting the effects of warming is in many cases a complex, far from trivial task.

During outbreak events in forested areas, it is hypothesized that herbivore-plant interactions and impacts will intensify with ongoing climate changes, leading in some cases to more or less permanent shifts in understory communities (Tenow, 1972; Jepsen et al., 2013; Karlsen et al., 2013). This study addresses two central questions that will help us understand how the impacts of current herbivore outbreaks and outbreaks of the future will affect plant communities and vegetation boundaries during climate warming and at elevated CO₂. We ask firstly, how does host choice affect herbivory during an outbreak? Secondly, will future climatic changes affect herbivore pressure (i.e., as in density of larvae per percent cover of a species)? To examine these questions, we investigated how future global climate change factors will affect consumption rates during an outbreak of the autumnal moth *Epirrita autumnata* (Borkhausen, Lepidoptera: Geometridae) by using a general model of larval herbivory validated from experimental simulations of expected future changes in temperature and atmospheric CO₂ concentrations. In Sub-arctic Fennoscandia, populations of such forest defoliating insect species sometimes grow to outbreak densities and when their host trees are defoliated they search for food at ground level on dwarf shrub communities (Tenow, 1972). Here we introduce a simple and general mechanistic mixed model combining climate-dependent host plant choice and consumption. This model can be applied to any insect that shows outbreak dynamics with larval herbivory and limited larval dispersal. Using unique field collected data we are able to test its validity and predict shifts in herbivory among species. Data were collected on *E. autumnata* larval densities during an outbreak, and by assessing the impacts on plants in experimental plots subjected to ambient and expected future elevated CO₂ and temperature treatments in Sub-arctic Sweden. The host preference model would predict shifts in feeding choice in mixed shrub plots.

2. Material and methods

We developed a model based on the hypothesis that future climate change scenarios (including elevated CO₂ and temperature) will influence host preference of an insect herbivore at high densities through intraspecific competition (i.e., larval crowding and consumption).

2.1. Host preference in relation to larval crowding rates

57% of Lepidoptera, among them *E. autumnata*, are polyphagous (Zalucki et al., 2002) and hence, potentially able to feed on different plant species. In many forest Lepidoptera, host preference is strongly linked to limited, free-moving late instar larval dispersal, as opposed to passive ballooning in neonate larvae (Ward et al., 1990; Carrière, 1992; Robinson & Raffa, 1997). For *E. autumnata*, there is evidence of limited dispersal in late instars (Tanhuanpää et al., 2000). Here our definition of limited dispersal is of the order of 5 m given the small temporal and spatial scales associated with starving late instar larval movement in the experimental system. Hence, in the model, larvae aggregate within or avoid patches with a certain cover of a plant species. Preference for a host plant is defined as the rate at which larvae move to forage (i.e., crowd) or away from a specific location with a certain host plant

composition. We surveyed vegetation at two consecutive survey times. L_1 and L_2 represent counts of larvae at times 1 (initial time) and 2 respectively (immediately before pupation, see below for data collection). As larval population movement takes place in continuous time, larvae at the site were expected to crowd (i.e., aggregate in a patch) according to an exponential expression with an intrinsic growth rate (Lombaert et al., 2006) $r = a + bR$.

Accordingly, $\lambda = er = L_2/L_1$ is the finite crowding rate of larvae at the site. R is the host percent cover in the site. a is a parameter describing natural crowding rate in the absence of the host, and b is the rate at which crowding changes with host cover, although other coefficients can be added to account for the dependence on environmental variables (see *Statistical analysis* below). Thus, $r > 0$ and $r < 0$ denote crowding or avoidance of other larvae, respectively, while $b > 0$ and $b < 0$ point towards preference for, or rejection of the host, respectively.

If two plant host species x and y coexist, the crowding rates of their consumers will be $r_x = a_x + b_x R_x$ and $r_y = a_y + b_y R_y$, respectively. If their percentage covers are complementary (that is, $R_y = 100 - R_x$), several preference responses are possible:

- 1 If there is preference towards one plant species and rejection towards the other ($b_x < 0 < b_y$ or $b_x > 0 > b_y$), preference is given to the host providing the higher r , independently of its cover. In an illustration depicting crowding rate r as a function of the resource R_x , the crowding rates for both hosts will not cross.
- 2 If any of the two scenarios, $b_x b_y > 0$ or $b_x b_y < 0$, is true, then host preference is defined by the point where both crowding rate responses cross in that graph. Crowding will avoid mixed stands and overall preference will be described by a v-shaped relationship. In the first scenario, host preference will shift from y to x as x cover increases (Fig. 1a). In the second scenario preference will shift from x to y . Equating both crowding rates, we obtain the critical breakpoint defining shifting preference between species x and y :

$$p_{xc} = \frac{a_y + 100b_y - a_x}{b_x + b_y}$$

However, if $r < 0$ at any range of host densities, larvae will move towards other sites which present a cover that satisfies crowding conditions. If $b_x b_y > 0$, the constraint $r > 0$ will determine that susceptible sites will be those with $R_x > -a_x/b_x$ and $R_x > -a_y/b_y - 100$.

2.2. A Gompertz model of herbivory

Many biological interactions have been described by density-dependent, Gompertz growth dynamics. In population ecology, studies with a mechanistic basis are rare (Geritz and Kisdy, 2004), but Gompertz growth has also been used to describe the dynamics of insect outbreaks (Dennis and Taper, 1994; Karban and de Valpine, 2010), and only once as a model of resource depletion in insect outbreak systems (Økland and Bjørnstad, 2006). In both cases Gompertz dynamics are derived and tested from statistical rather than mechanistic assumptions.

Gompertz growth is generally defined by a double-exponential equation. Specifically, for Gompertz decay, the equation takes the form

$$X_t = X_i \exp(g(1 - e^{-ht})) \quad (1)$$

where X_i is a state variable at time i , t is the time lapse starting from time 1, and $g < 0$; $h > 0$ or $g > 0$; $h < 0$ are parameters of the equation.

In this section, to discern the role of consumption versus larval crowding on the defoliation of host plants during an outbreak, we derive a mechanistic model of herbivory for Gompertz decay in resources that accounts for the observed patterns in resource consumption by *E. autumnata* larvae, but can be generalized to other herbivorous insects. The model is a 2D (resource and larvae) differential equation autonomous system:

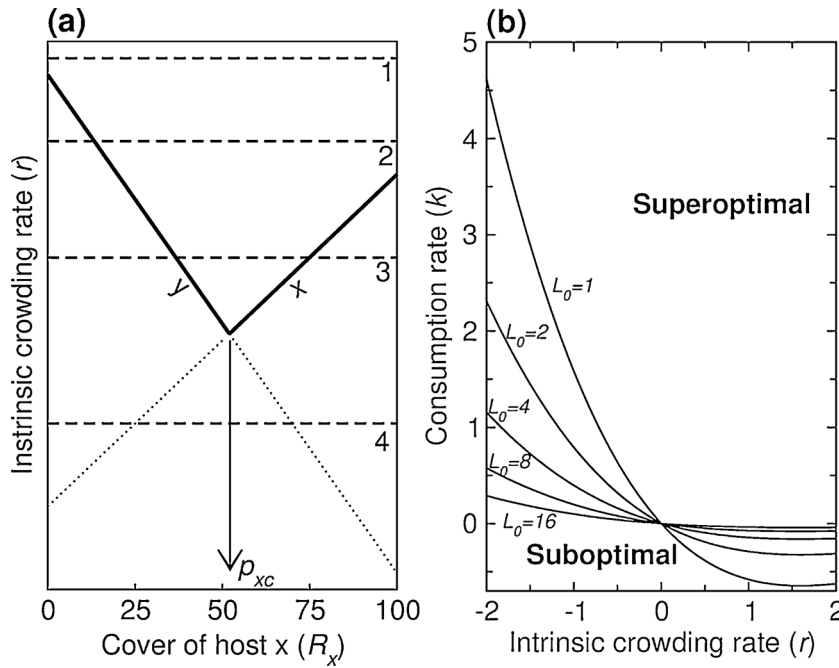


Fig. 1. Model for host preference and herbivory. (a) Host preference model, describing the relationship between host plant cover and larval crowding rates when two potential hosts attract larvae ($b_x, b_y > 0$) and coexist. Bold solid lines: Dominant crowding rate response. Thin solid line: Non-dominant response. Dashed lines: theoretical position of the zero crowding rate isoline. The breakpoint p_{xc} indicates a shift in host preference. The position of the zero crowding isoline conditions the attraction towards hosts: 1. Avoidance of both hosts. 2. Host x is avoided, and crowding only occurs at high y covers. 3. Avoidance of plots where both hosts coexist. 4. No avoidance in any combination of host covers. (b) Optimal herbivory. Curves represent optimal consumption rate k_c (Eq. 6) balancing crowding for different initial numbers of larvae L_1 . Superoptimal ($k > k_c$) and suboptimal ($k < k_c$) regions above and below the curves show areas where overall herbivore pressure in the patch increases or decreases, respectively.

$$\frac{dR_t}{dt} = -kL_tR_t; \frac{dL_t}{dt} = rL_t \quad (2)$$

where $k > 0$ represents the consumption rate per larva (see *Calculating consumption rates* for further development). R and L are resource and larval abundance (as defined in the previous subsection), r stands for the crowding rate which indicates host preference and depends on the initial plant cover, as calculated in the previous section, and environmental factors (see *Statistical analysis* below). Integrating the second equation in system (2) and separating variables, the system is integrated into:

$$R_t = R_1 \exp(-k(e^{rt}-1)L_1/r) \quad (3)$$

Therefore, we recover Eq. (1) (aka the Gompertz equation) for the resource dynamics.

2.3. Calculating consumption rates

To calculate consumption rates, we first consider herbivore pressure at a certain time as $P_t = L_t/R_t$, measured in this study as insects per percent host cover at time t . Using Eqs. (1) and (3), and taking logarithms, the resulting growth rate in herbivore pressure over the sampling interval time is:

$$\ln(P_t/P_1) = k(e^{rt}-1)L_1/r - rt \quad (4)$$

Using an arbitrary time scale corresponding to the sampling lapse, $t = 1$, the realized consumption rates are calculated as:

$$k = \frac{r(\ln(P_2/P_1) + r)}{L_1(e^r - 1)} \quad (5)$$

Three specific scenarios arise from these equations:

- (1) In the absence of larval movement, $r = 0$, $\lim_{r \rightarrow 0} k = \ln(P_2/P_1)/L_1$, and Eq. 4 becomes $\ln(P_2/P_1) = kL_1$.
- (2) In the absence of consumption, $k = 0$, therefore Eq. 4 becomes $\ln(P_2/P_1) = -r$.
- (3) In conditions of optimal behaviour, larval populations migrate to minimize competition and maximize resource availability ($A = 1/P$) along time. In that case, no resource reduction takes place (i.e. $\ln(P_2/P_1) = 0$). Hence, optimal consumption is given by:

$$k_c = \frac{r^2}{L_1(e^r - 1)} \quad (6)$$

where k_c is an optimal consumption rate in that migration and consumption balance each other and resource availability is kept constant through time (Fig. 1b). Negative differences between the realized consumption rates and optimal ones due to crowding or feeding preference indicate whether overall larval consumption in the patch is suboptimal (i.e., below that necessary to balance crowding, so $k - k_c < 0$) or superoptimal ($k - k_c > 0$), pointing towards reductions, and increases in herbivore pressure, respectively. Therefore, Eq. 5 shows that variations in herbivore pressure can be ascribed to crowding, which in turn reflects differences in host composition and environmental factors, such as temperature and CO_2 .

The Gompertz model can be used to calculate consumption and immigration (crowding) rates based on the host preference r by herbivore larval populations derived from the previous model. In communities composed of different potential hosts, the combined host preference-Gompertz model predicts: 1) shifts in crowding rates according to the relative cover of each host, and 2) calculation of realized consumption rates following Eq. 5. However, the model itself can encompass situations in all the three specific scenarios above (i.e., no preference and/or no consumption). Hence, its generality makes it suitable for any situation in which a short-dispersal herbivore can feed on one or two competing species, including lack of interaction between the plants and the insect or lack of limited larval dispersal.

2.4. Study site and data collection

Data were collected during an outbreak of *Epirrita autumnata* in 2004 at Abisko, Sweden (68.35°N, 18.82°E, 360 m a.s.l., well below the treeline of 500–600 m a.s.l.). The larvae hatch in spring at the time of *Betula pubescens* var. *pumila* (L.) Govaerts (mountain birch, their main host) bud burst and forage for approximately one month on the mountain birch (Tenow, 1972). When the birch leaves have been depleted in outbreak years, larvae search for other food sources by descending to the ground to feed on shrub vegetation before pupating (Tenow et al., 2004). The site, with a Sub-arctic montane climate, was based in a mountain birch forest with a ground layer dominated by a dwarf shrub community composed mostly by the deciduous *Vaccinium myrtillus* (bilberry) and two evergreen shrubs, *Vaccinium vitis-idaea*

(lingonberry) and *Empetrum nigrum* (black crowberry) plus other deciduous shrubs (*Betula nana*), grasses and herbs (e.g. *Deschampsia flexuosa*, *Cornus suecica*). Both *Vaccinium* species and *E. nigrum* compete for space in the regeneration process after disturbance (Phoenix et al., 2000). We investigated larval numbers and percentage (%) cover of vegetation in an experimental system (established in June 2000) that was entering its fifth growing season of treatment during the insect outbreak of June 2004. The experimental system employed 1.5 m² Open Top Chambers (OTCs) to elevate CO₂ to 730 ± 25 ppm (versus 377 ppm ambient) using a fan sourced air supply injected with pure CO₂. Warming was controlled with soil heating cables and above canopy infrared lamps that elevated temperature by 5 °C (see Olsrud et al., 2004; Svensson et al., 2018). In this study we used six replicate plots per treatment, based around fully randomized experimental setup where the response of the dwarf shrub plant community was investigated to the following treatments i) Ambient conditions; ii) Elevated CO₂; iii) Elevated temperature; iv) Elevated CO₂ in combination with elevated temperature.

Larval numbers and vegetation cover of plant species were assessed within a 0.34 m² area within each chamber. Larvae were free to move between plots via the space between the chamber and ground or they could climb the chamber walls. They entered the plots post birch defoliation in surrounding areas and were counted (22nd June and 1st July 2004) from three 15 × 15 cm quadrats per plot (total plot size investigated 0.34 m² with chamber footprint of 1.5 m²). All larvae were returned to their respective collection areas upon completion of counts. For each quadrat, we also estimated reductions in the percentage cover of dwarf shrubs (bilberry, lingonberry and black crowberry). This was done visually to the nearest 5% on both dates as a surrogate of biomass removal for all treatments.

In this study, we focused on herbivory and food preference related to the three dominant shrub species with all other vegetation types including grass, herbs, lichens and mosses classified as “Other species”. The mountain birch trees in the experimental area had almost totally been defoliated (95–100 %) both above and around the sites by the time measurements began with larvae searching for food in the understorey shrub area.

2.5. Statistical analysis

To detect shifts in host preference, segmented linear regression models (Toms and Lesperance, 2003) were performed. The models relate host cover and the environmental variables temperature and CO₂ to intrinsic crowding rates with the use of the R statistical package (R Development Core Team, 2011). Since the cover abundances of all species suffer from multicollinearity, we performed a “detection of breakpoints” test on host preference by reducing the dimensionality of the system into two groups: evergreen shrubs and a group with the rest of the species, which include both bilberry and “other species”. Due to the presence of some plots with zero larvae, we used the crowding rate of larval abundance as $r = (L_2 + 1)/(L_1 + 1)$. This modification did not significantly alter the assumptions of normality and homoscedasticity, and allowed us to use the linear model with a full factorial design. Crowding rates may, however, depend not only on host cover, but may also be related to the initial number of larvae L_1 due to density-dependence, in which case our assumption for the exponential model for crowding, which depends only on host cover, would be invalidated. Post-hoc analysis on all 72 sampled quadrats (from 24 plots) showed similar initial larval densities ($\ln(L_1 + 1)$) and density variability at the beginning of the survey (Tables S1 and S2 and Fig. S1) in all plots regardless of treatment or species cover. There was also an absence of collinearity between initial evergreen species cover at the beginning of sampling in 2004 and either temperature (polyserial correlation $\Omega = 0.39$, $P = 0.37$) or CO₂ ($\Omega = 0.22$, $P = 0.66$) treatments, indicating, again, that initial host densities had not been affected by previous history in the environmental signature of the plots.

Thus, the full factorial segmented linear model, dependent on host composition (Kuussaari et al., 2000), and environmental factors, takes the form (Toms and Lesperance, 2003):

$$r = b_0 + b_{11}R_x + b_2T + b_3C + b_4TC + \varepsilon \quad \forall R_x \leq p_{xc}$$

$$\leq p_{xc} \quad r = b_0 + b_{11}R_x + b_{12}(R_x - R_{xc}) + b_2T + b_3C + b_4TC + \varepsilon \quad \forall R_x > p_{xc} \quad (7)$$

where r is the response variable (crowding rate), and R_x , T , and C define the covariates evergreen cover, temperature and CO₂, respectively. b_{11} describes the first and $b_{11} + b_{12}$ the second slope (in the v -shaped relationship) for the evergreen cover. $b_i \forall i \geq 2$ represent the coefficients for the environmental main effects and second and third order interactions, and ε stands for the independent, additive error with zero mean and constant variance. Model fits were developed using the package “segmented” (Muggeo, 2009). We performed stepwise model selection to select the most parsimonious model through AIC values.

We tested the accuracy of the previous segmented regressions by implementing thin plate splines for the crowding rates using the package “fields” (Nychka et al., 2014) over two selected groups: evergreen shrubs and bilberry. They were performed over a Cartesian coordinate system with the two shrub groups (bilberry versus evergreen) as covariates to test for potential multicollinearity, and converted back into a barycentric coordinate system with bilberry, evergreen and other species as covariates.

Consumption rates were calculated following Eq. (5) for bilberry and evergreen species. Since consumption rates followed quasi-Poisson distributions (Fig. S2), we used generalized linear models with quasi-Poisson error structure to determine the effect of crowding rate, temperature and CO₂ on the consumption rates of both shrub groups and the logarithmic growth rates of herbivore pressure (insects per % species cover). The initial larval densities were pooled for each significant treatment scenario using their geometric mean.

When resource saturation takes place, larval populations following Gompertz dynamics are expected to balance movement with consumption, defined by the optimal consumption k_c in Eq. 6. We tested deviations from optimal behaviour, and hence, realized reductions in herbivore pressure, by calculation of $k - k_c$ (see Calculating consumption rates). Finally, thin plate splines were also used to map those scenarios of host cover and treatment where consumption was lower than expected under an optimal, balanced model of herbivory (i.e., $k - k_c < 0$). All thin plate splines were performed over polynomials of degree 3.

3. Results

Plant cover dictated larval crowding rate, which determined host choice. This clearly contrasts with the case where crowding rate is independent of plant cover (Fig. 1a, lines 1–4). Our results show a strong larval affinity towards mono-specific stands, especially towards those covered by bilberry, and avoidance of mixed stands (i.e., those where bilberry and evergreen shrubs coexist in similar proportions), following a v -shaped pattern for host preference (i.e., dominant crowding rate response, bold line in Fig. 1a). Evergreen species were preferred when their cover represented > 40% of the community (Fig. S3, $F = 7.07$, $P < 0.001$) and, against our initial hypothesis, this was independent of the climate change factors tested (temperature ($F = 0.72$, $P = 0.40$) and CO₂ ($F = 1.10$, $P = 0.30$), Tables S1–S2). Larval crowding manifested when evergreen cover was less than 26% or more than 70%. In between, larvae left the plots (Figs. 2a, S3). The presence of a critical shifting breakpoint in larval preference at 40% of evergreen species cover was confirmed by the thin-plate smoothing spline, indicating that species other than evergreen shrubs or bilberry play no perceptible role in larval preference (Figs. 2a, S3).

Temperature was the only significant environmental variable tested that had any effects on consumption: there was lower consumption of the deciduous species *V. myrtillus* (bilberries, $P < 0.05$) at elevated

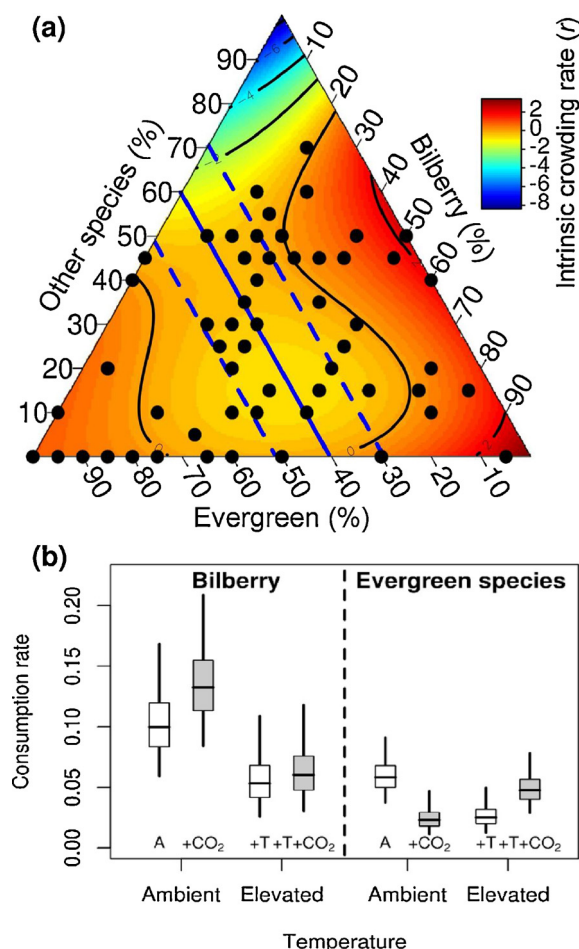


Fig. 2. Crowding and consumption rates in *E. autumnata*. (a) Triangular thin plate spline of crowding rates over the relative cover of three plant groups considered. Black dots represent the plots surveyed. The solid blue line is the position of the breakpoint in the segmented regression of crowding rate vs. evergreen cover (Fig. S3). Dashed blue lines are the confidence intervals of the breakpoint in the segmented regression. (b) Calculated consumption rates resulting from the quasi-Poisson generalized linear model in Eq. 5 for different temperature and CO₂ scenarios. Boxes and solid vertical lines depict 50% and 95% confidence intervals. Grey boxes depict elevated CO₂ scenarios. +T = Elevated future temperature; +CO₂ = Elevated CO₂; +T + CO₂ = Elevated temperature plus elevated CO₂. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

temperature (Table 1). The consumption level under this treatment reached values similar to those found for evergreen species under ambient temperature (Fig. 2b, Table 1). However, for evergreen species,

temperature interacted with CO₂: the consumption of evergreen species was reduced when the community was exposed to future temperature and CO₂ alone but there was no effect when both these factors were applied together (Fig. 2b).

Under current ambient climatic conditions, higher *V. myrtillus* consumption rates were linked to a preference towards mono-specific stands, which was reflected in an increased herbivore pressure on pure bilberry stands. However, in a warmer climate scenario herbivore pressure was partially eased (Figs. 3 and 4, Table 1). The importance of both crowding and consumption mechanisms is reflected by the statistical fit of our Gompertz model (Fig. 3, Table 1). The Gompertz model predicts that the balance between crowding and consumption will determine herbivore pressure, and follows a log-log linear relationship with crowding rates in the absence of consumption (see *Calculating consumption rates*). Our statistical fit validates both mechanisms as contributors to herbivore pressure, providing a faster than linear increase for herbivore pressure in log-log axes (Fig. 3). A future warmer climate scenario clearly shows suboptimal consumption, and thus, released herbivory pressure on bilberry in mixed vegetation areas (Fig. 4),

4. Discussion

Overall, the statistical fit of the data based on the mixed model predicts that: 1. shifts (i.e., increases and decreases) in herbivore pressure on the potential hosts in monocultures following increasing temperatures; 2. decreased herbivore pressure on the host in mixed stands is most likely to occur as a result of climate warming.

We initiated this study to assess the importance of host preference during an outbreak of *E. autumnata* and whether future climatic changes (elevated CO₂ and temperature) will affect herbivore pressure. Regarding CO₂ the only observed effect was that consumption of evergreen species was reduced when the community was exposed to elevated CO₂ alone but there was no significant effect when in combination with elevated temperature.

Pooling all plots together, our study found that consumption rates on bilberry were not significantly affected either by warming or CO₂, agreeing with recently reported results during the 2003–2004 outbreak in Abisko (Svensson et al., 2018). CO₂ has been previously hypothesized to alter palatability on a per-species basis by changing foliar C:N ratios or its production of consumption-inhibiting secondary compounds (Lindroth, 1996). Our analysis shows that CO₂ effects on consumption rates in different shrubs are present, but not significant. Hence, we can not reject that CO₂ has no effect on consumption. A possible balance between both increases in carbon storage compounds and secondary metabolites (the well-known carbon nutrient balance hypothesis, *sensu* Bryant et al., 1983) precludes a clear response. A significant interaction between CO₂ and temperature, as reflected in the apparent distinctive consumption patterns of evergreen shrub consumption, further complicates a clear interpretation in regards to CO₂ in the context of this study.

Table 1

Summary of the quasipoisson generalized linear model (with a logarithmic link function) used to calculate consumption rates in bilberry and evergreen species. Higher-order non-significant interactions were discarded. The three last columns show average deviations from optimal conditions ($k-k_c$) where consumption balances crowding. A = Ambient conditions; +T = Elevated future temperature; +CO₂ = Elevated CO₂; +T + CO₂ = Elevated temperature plus elevated CO₂. Consumption rates are shown in percentage cover per larva during a 10 days interval.

Species	Source	Df	Estimate	Std Error	P(> t)	Scenario	k-k _c	P(> t)
Bilberry	Intercept		-2.152	0.173	< 2e-16 ***	A	0.098	0.0001***
	T effect	1	-0.718	0.302	0.02*	+T	0.021	0.036*
	Error	70						
Evergreen	Intercept		-2.842	0.228	< 2e-16 ***	A	0.037	0.21
	T effect	1	-0.84	0.415	0.047*	+CO ₂	0.011	0.812
	CO ₂ effect	1	-0.93	0.429	0.034*	+T	0.031	0.36
	Interaction	1	1.567	0.606	0.012*	+T + CO ₂	0.021	0.464
	Error	68						

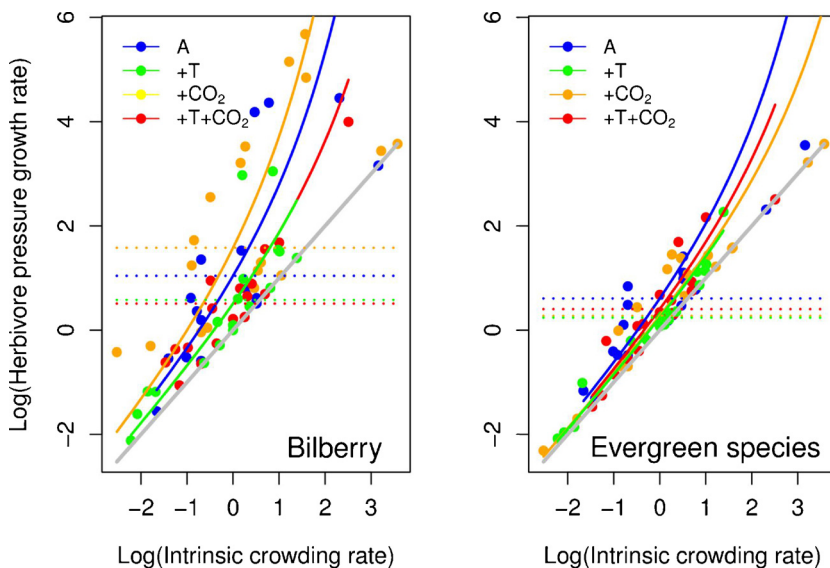


Fig. 3. Herbivore pressure depends both on crowding and consumption. Quasi-Poisson model regressions show the dependence of the growth rate of herbivore pressure on the crowding rate (Eq. 4) for both host species. A = Ambient conditions; +T = Elevated future temperature; +CO₂ = Elevated CO₂; +T + CO₂ = Elevated temperature plus elevated CO₂. Initial number of larvae is included in the equation as the geometric mean. Gray line: Expected herbivore pressure in the absence of larval movement. Horizontal coloured lines: Expected herbivore pressure in the absence of consumption (see Calculating consumption rates).

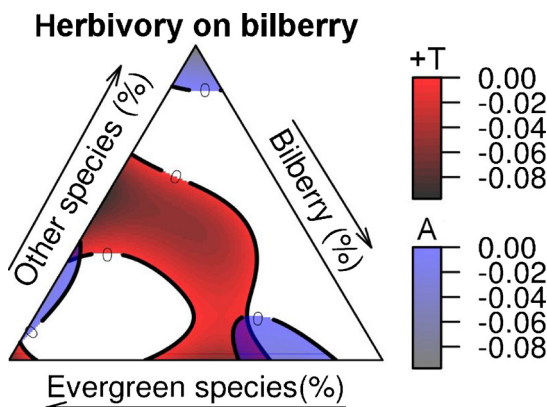


Fig. 4. Consumption on bilberry under climate change is reduced in mixed stands (coexistence of the three host species). Reduction of herbivory on bilberry under current and future environmental conditions: coloured areas show suboptimal bilberry consumption (i.e., negative differences between realized and optimal consumption rates, $k - k_c < 0$) (see Calculating consumption rates). White areas depict superoptimal consumption. Under ambient conditions, suboptimal consumption only scarcely occurs in marginal areas like some stands with large dominance of bilberry. However, under future warmer scenarios, strongly suboptimal consumption of bilberry is more prevalent in mixed stands. A = Ambient conditions; +T = Elevated future temperature.

Regarding temperature, we detected significant reductions of bilberry consumption in mixed evergreen-deciduous shrub plots under warming (Fig. 4), but not significant increases in bilberry-dominated plots. This result does explain the overall reduction in bilberry consumption when all plots are pooled in the analysis. Yet, in ambient conditions, herbivory on bilberry was higher than on the evergreen shrubs, confirming previous observations regarding the higher palatability of the first (Svensson et al., 2018).

Our study also differs from that of Barrio et al. (2016) who studied the effects of elevated temperature on non-outbreak insect activity, yet some common findings were observed. In both studies, larvae shift their food preference, described by the v-shaped host choice function. For Barrio et al., herbivory shifted towards higher consumption of more nutritious hosts with warming. In contrast, in the current study and under outbreak conditions the opposite effect was observed. The v-shaped function indicates that, during an outbreak, larvae choose food according to quantity, rather than tissue quality (Ruohomäki et al., 2000), and the effect can be dependent on larval densities and the

herbivore species (Birkemoe et al., 2016). Although larvae preferred to feed on bilberry in current temperature conditions (as in Svensson et al., 2018), there were substantial crowding levels also observed on plots largely dominated by evergreen shrubs. However, mixed vegetation stands were generally avoided. Although not measured in this study, switching between host plants has been previously shown to indicate a capacity to overcome host-induced resistance (Kaitaniemi et al., 1999).

Hence, our model also shows that herbivore pressure during outbreaks depends both on the host-dependent larval movement (or preference towards a host) and the actual temperature-driven consumption. The Gompertz model confirms that preference translates into higher consumption per larva in bilberry for the current climate scenario. Although larvae are still attracted to bilberry under warmer temperatures, their individual consumption rates are halved to sub-optimal levels, reducing overall herbivore pressure on this host in mixed deciduous-evergreen areas. This result partly contradicts previous findings that warmer temperatures accelerate insect growth and consumption (Bale et al., 2002; Birkemoe et al., 2016), but agrees with Barrio et al.'s (2016) findings that the performance of invertebrate herbivores is reduced under warmer conditions. The difference here in the current study is that measurements were undertaken during an insect outbreak.

Two main assumptions govern our model: first, crowding is affected by environmental conditions (temperature and CO₂) and resource availability; two, this dependence on resource availability is general in that it does not need to be either linear or monotonic (which would in fact be two extra specific assumptions) and can shift preference between different host species. As shown in Fig. 3, failure to comply with these assumptions (either lack of larval crowding, or zero consumption) would have generated herbivore pressure models unable to fit the field data. These assumptions entail that consumption is mostly dependent on the local awareness or information that larvae have on their surrounding resources (Gamarra, 2005). Consequently, the model resource and herbivore dynamics are limited at the small spatial and within-seasonal temporal scales, where birth and death processes of both resource and herbivore, typically used for among-year population dynamics, are not considered.

Several studies have observed vegetation changes in the north (e.g. Callaghan et al., 2013; Post et al., 2009; Tømmervik et al., 2004) and others suggest increased dwarf shrub growth and success in response to future warming in the Arctic (Van Wijk et al., 2003; Elmendorf et al., 2012), including bilberry growth (Richardson et al., 2002). Furthermore, envelope bioclimatic models confirm that more thermophile

plant species including bilberry will expand their ranges as the climate warms (Tømmervik et al., 2004; Milbau et al., 2009). Although, contrary to Barrio et al.'s (2016) study, we found a release of herbivory on the preferred shrub host plant *V. myrtillus* in mixed stands under predicted future climate conditions. However, for the first time, we show that under warming herbivory could potentially promote expansion of this plant species via a reduction in its selection by the autumnal moth in areas with mixed deciduous/evergreen shrub composition. This of course depends on the severity and the distribution of outbreaks as during very intensive outbreaks the insects can consume all available vegetation within a given area. At the landscape level, effects will likely operate most strongly where evergreen and deciduous plant species are mixed, such as range boundaries. Thus, any realistic attempt to predict changes in these locations will require the inclusion of these effects in large-scale envelope models of species distributions. At smaller scales, if Gompertz trends in resource depletion occur in evenly mixed plant communities, bilberries will be exposed to less herbivory. Consequently, as stated by Lindroth (1996) as a general CO₂ influence on host plants, and Haukioja (2005) for the mountain birch community, bilberry may reduce allocation to defensive secondary compounds in favour of growth. This will likely favour the establishment and faster expansion of the bilberry in those areas that currently have mixed vegetation. In turn, larvae will increasingly shift back towards more consumption as it becomes dominant and exposed to further outbreaks. Yet, competitive processes between shrubs may distort this patterns during the time lapse between successive outbreaks. In the end, inferring community-level projections from such experiments is challenging and larger-scale studies are required (Lindroth, 1996; Birkmoe et al., 2016).

The parameterization of our model is based on the specific scenarios under which *E. autumnata* herbivory occurs in the field, and is founded on a small set of plots. Validation of the model parameters for this particular system can be challenging, due to the 9–10 year typical frequency of *E. autumnata* outbreaks in Fennoscandia (Tenow, 1972) and the complexity of factors and logistics regarding the use of OTCs for environmental manipulation. A practical approach will depend on the long-term continuation of the Abisko research station and objectives, combined with emergency protocols to sample larval herbivory when the outbreak arrives, and possibly an increase in the sampling size (including additional OTCs).

Notwithstanding the challenges of validation, the model is general in its formulation. First, it can be applied to the forest-tundra transition in Fennoscandia, where *E. autumnata* outbreaks show dramatic effects. Second, it includes situations where larval switching preferences are absent, in which case Gompertz decay would be absent. Thus, the generality of the model allows its application to other herbivore insects undergoing large population fluctuations, either with limited mature larval movement driven by host preference, like *Lymantria dispar* (Mauffette and Lechowicz, 1984), *Choristoneura rosaceana* (Carrière, 1992), *Thyridopteryx ephemeraeformis* (Ward et al., 1990) and *Malacosoma dissitria* (Robison and Raffa, 1997) – or without it. Although the model needs to be tested in other areas, it is a warning against the lack of both movement and consumption dynamics in any large-scale species composition modelling study, particularly ecosystems exposed to insect outbreaks or any other significant biotic interactions.

Author contributions

JGPG developed the theoretical Gompertz and preference model and statistical analyses and wrote the manuscript, DG-J initiated and managed the data collection and co-wrote the manuscript. HB contributed to the manuscript text and advised on sampling and analysis. TVC was instrumental in helping to set up the experiment via Abisko Scientific Research Station with colleagues at Marine Biological Laboratory, Woods Hole (Frank Bowles, Jerry M. Melillo and others). TVC also contributed to manuscript development.

Conflict of interest

The authors are not aware of any conflict of interest.

Acknowledgments

We thank Professor. Christer Jonasson (formerly at Abisko Scientific Research Station) for logistic support, particularly from Louise Tränk. We are grateful to Prof. Jerry Melillo and Dr. Frank Bowles for access to the experimental plots. Prof. Brita Svensson and Dr. Bengt Carlsson are thanked for advice on the experiment and data collection. DG-J thanks IBERS, Aberystwyth University for support given to participate in this work. Georg Wohlfahrt and an anonymous reviewer kindly helped to fine-tune the manuscript.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.agrformet.2018.08.016>.

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